

A STUDY OF SOME ANT LARVÆ, WITH A CONSIDERA-
TION OF THE ORIGIN AND MEANING OF THE
SOCIAL HABIT AMONG INSECTS.

7a

By WILLIAM MORTON WHEELER.

Reprinted from
PROCEEDINGS OF THE AMERICAN PHILOSOPHICAL SOCIETY
Vol. LVII, No. 4, 1918.

A STUDY OF SOME ANT LARVÆ, WITH A CONSIDERATION OF THE ORIGIN AND MEANING OF THE SOCIAL HABIT AMONG INSECTS.¹

By WILLIAM MORTON WHEELER.

(Read April 19, 1918.)

The care lavished by ants on their brood is a matter of such frequent and easy observation that it has always excited wonder and comment. When a colony is disturbed at the height of the breeding season the brood is at once seized and carried to a place of safety, and when more closely observed in artificial nests the behavior of the workers is seen to be very largely a constant round of the four different activities of feeding, licking, transporting and defending the young. Swammerdam says in that wonderful volume, the "*Biblia Naturæ*" (1737-1738): "Incredible *στοργή* et cura Formicæ educant summamque dant operam, ne vel tantillum quod spectet eorum Vermiculorum educationem atque nutritionem omitant"—"with incredible affection and care the ants bring up their vermicules and omit not the least thing appertaining to their education and nurture." He intentionally uses the word *στοργή*, from the verb *στέργειν*, to express his belief that love or affection impels the ant to care for her young, since there is no Latin equivalent for a term which to the Greek meant the affection of the members of a human family for one another as distinguished from other forms of "tender feeling."² And observers since Swammerdam seem uniformly to have agreed with him, though more modern writers often use such terms as "care of the brood" as more suited to the present colorless and noncommittal stage of natural history.

Now it must be conceded that Swammerdam's statement calls

¹ Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University. No. 147.

² Plato in the "*Laws*," 754B, uses the verb in its typical Greek sense when he says: *παῖς στέργει τε καὶ στέργεται ὑπὸ τῶν γεννησάντων*.

Reprinted from Proceedings American Philosophical Society, Vol. lvii., 1918

attention to a real problem, but one that belongs to the psychologist and not to the biologist. I am quite willing to admit that there may be in ants some feeble analogue of the parental feelings of man and the highest animals, but as a biologist I am bound to seek and if possible to find some ethological or physiological basis for the ant's behavior toward her brood. Like other students of insects I have, no doubt, often taken too much for granted and have unquestionably committed the eighth deadly sin, called by the orthodox behaviorists "anthropomorphism," not once but many times. By way of partial penance I offer the following paper.

I confess that I took the Swammerdamian conception for granted till recently, while studying a collection of ants made in the Belgian Congo for the American Museum of Natural History by my friend Mr. H. O. Lang. I came upon some facts which seem to throw a flood of light on the true meaning of the relations of ants to their brood. These relations now appear to me so simple and unequivocal that I find difficulty in understanding how they could have remained so long unperceived, especially as a host of other facts had been insistently pointing in the same direction. Our blindness seems to have been due to regarding the adult ants as the only active factors in the brood relationship. We supposed that the larvæ, probably because they are such sluggish, legless maggots, were merely the inert and passive objects of the feeding, licking, transportation and protection. One result of this assumption has been a general neglect of the study of larval ants. Even their morphology has received little attention. There are a few valuable papers by Berlese (1901), Karawaiew (1896) and Pérez (1902) on the metamorphosis of ants, a single paper by Emery (1899) devoted to the external characters of the larvæ in a selected series of species and a number of scattered descriptions and figures, published mainly for taxonomic purposes, by myself and others.

I regret that in the past I failed to study the larval ants more closely and more continuously, especially as the meaning of some of the unpublished records in my notebooks of 1899 and 1900 is clear to me only now after the lapse of nearly twenty years. When I took up my work at the University of Texas in the fall of 1899 as a morphologist accustomed to well-furnished northern and European

embryological and anatomical laboratories and libraries, I found so little apparatus for the work in which I had been trained, that I fell into a peculiar listlessness and was for some weeks unable to concentrate my attention on any subject that seemed worthy of investigation. One day, while I sat on the bank of Barton Creek, near Austin, in the very spot where, as I later learned, MacCook had worked on the famous agricultural ant (*Pogonomyrmex molefaciens*), I happened to see a file of cutting ants (*Atta texana*), each with its piece of leaf poised in its mandibles. I vividly remember the thrill of delightful fascination with which I watched the red-brown creatures trudging along under their green loads, and it seemed to me that I had at last found a group of organisms that would repay no end of study. At that time there was no active myrmecologist in the country. MacCook had completed his work and Pergande was no longer deeply interested in the ants. Prof. Emery, however, and later Prof. Forel extended helping hands to me and forthwith sent me their numerous and important publications, and several of my students, notably C. T. Brues, A. L. Melander, C. G. Hartman and W. A. Long, never wearied of accompanying me on long excursions into the dry, sunny woods and canyons about Austin.

For a time I was greatly interested in the habits of three large ants of the primitive subfamily Ponerinae, *Odontomachus clarus*, *Pachycondyla montezumæ* and *Lobopelta elongata*, which are common in Central Texas. I was able to show that their peculiar tuberculate larvæ are not fed with regurgitated food, like the larvæ of more specialized ants, but with pieces of insects (1900). Concerning the feeding of the *Odontomachus* larva I published the following remark (p. 24):

These larvæ are placed by the ants on their broad backs, and their heads and necks are folded over onto the concave ventral surface, which serves as a table or trough on which the food is placed by the workers.

An unpublished note, the significance of which I did not appreciate at the time, refers to *Pachycondyla* and was recorded while I was studying the behavior of its extraordinary Phorid commensal, *Metopina pachycondylæ* (1901). It runs as follows:

As soon as the fragments of insects are placed on the larva's trough-like ventral surface, the latter is sometimes inundated with a copious, colorless liquid, which is at once eagerly lapped up by the attendant nurse.

I should now describe this behavior in the following words: As soon as the fragments are placed on its ventral surface, the larva discharges from its salivary glands a supply of secretion which is sometimes very abundant. This secretion, by means of a strong proteolytic ferment which it contains, digests the food extraintestinally and thus enables the larva to swallow and assimilate it, and at the same time serves in part as an agreeable draught for the nurse. The strong mandibles of the Ponerine larvæ are used for comminuting the insect food and thus preparing it for the action of the saliva. The larval feeding habits of our small northern species of *Ponera* and *Stigmatomma* are essentially the same as those of the Texan genera, as I showed in a special paper (1900a).

Within recent years I have examined the larvæ of a number of different Ponerinæ and have found them all to possess well-developed mandibles. All, in my opinion, except, perhaps, during their very youngest stages, are fed with fragments of insects, supplied directly by their nurses. In some species, the insect prey is probably given to the larva without previous dismemberment. I here describe and figure the young of three genera, *Myrmecia*, *Megaponera* and *Bothroponera*, as they differ considerably from one another and from all previously described Ponerine genera and will serve therefore to illustrate the diversity of larval structure within the subfamily.

Fig. 1 is from a photograph of the adult larva of *Myrmecia sanguinea*, one of the larger Australian bulldog ants, the most primitive of existing Formicidæ. It is milk-white, has the form of a vegetable marrow, with all the segments distinct, except those at the extreme posterior end of the body, the anterior segments are very slender and curved and the head is very small. The body is rather uniformly clothed with short, rapidly tapering, bristle-like hairs. Under a higher magnification the head (Fig. 2) is seen to have a projecting bilobed clypeus (*c*), broad, heavily chitinized, coarsely tridentate mandibles (*m*) and well-developed maxillæ (*x*) and labium (*l*), the former with two pairs of strongly chitinized peg-

then reach into its body cavity and devour its soft parts. The mandibles of the *Myrmecia* larva certainly show that it feeds on insect food.

The second larva (Fig. 3) is that of the "Matabele ant," *Megaponera fœtens*, of which Mr. Lang secured many specimens in the Belgian Congo. Arnold (1914) and others have shown that this

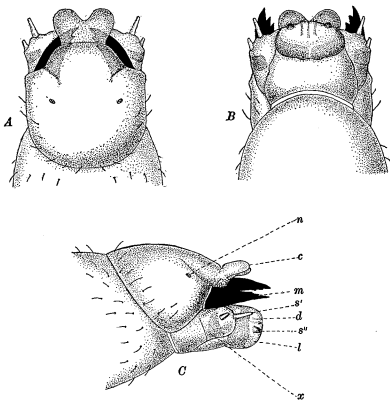


FIG. 2. Head of *Myrmecia sanguinea* larva. A, dorsal; B, ventral; C, lateral view; n, antenna; c, clypeus; m, mandible; x, maxilla; s, maxillary sensilla; l, labium; s'', labial sensilla; d, opening of salivary duct.

ant preys on termites, the bodies of which it carries home agglutinated in the form of pellets (Alluaud in Santschi, 1914). It is very restless and changes its nesting site frequently, so that it is obliged to carry its young about a great deal and for considerable distances.

The larva is cylindrical, covered with a very tough, opaque, grayish, hairless skin and furnished with long, falcate mandibles. The pupa is enclosed in a very tough, black cocoon. These peculiarities are evidently adaptations to exposure to the air and light, to the exigencies of frequent and protracted transportation and to feeding on the bodies of termites brought into the nest by the workers. Mr. Lang actually observed the exposure of the black cocoons to the sunlight, a peculiarity of behavior which I had also observed in certain Australian Ponerinæ of the genera *Diacamma* and *Rhytidoponera* (1915).

The third larva (Fig. 4), that of *Bothroponera sublaevis*, one of four species of the genus, which I collected in Australia, has a very broad elliptical body, with a short, stout neck, strongly folded over onto the ventral surface, which is somewhat concave. The integument is also hairless and of a peculiar opaque, gray color. The sides of the three thoracic segments and first abdominal segment are furnished with fleshy tubercles and the mouthparts are very highly developed. It is placed on its back by the nurses and fed with fragments of insects deposited on its trough-like ventral surface as in our North American Ponerinæ.³

The feeding of the larvæ with pieces of insect food is not, however, confined to the Ponerinæ. Miss Fielde and I have shown that one of the commonest Myrmicine ants of the North Eastern States, *Aphaenogaster fulva*, has the same habit. During late June, at the height of the breeding season, it is hardly possible to remove the stone covering a nest of this ant without finding one or more larvæ lying on their backs or sides in the act of feeding on the legs of flies or fragments of other small insects. Janet has observed simi-

³ Mayr described *Bothroponera* as a genus, but Emery, Forel and Santschi have been treating it as a subgenus of *Pachycondyla*. I return to Mayr's conception, because the adult, at least, of the Australian species of *Bothroponera* exhibits several peculiarities of behavior, such as the extrusion when captured of a mass of frothy bubbles from the tip of the gaster, and because of the structure of the larva, which is very different from that of *Pachycondyla* as will be seen by comparing Fig. 4 with my previously published figures of *P. montezuma*. The larvæ of *Diacamma*, *Leptogenys* and *Odontomachus* bear a greater resemblance to those of *Pachycondyla*. *Bothroponera* is, moreover, confined to tropical Africa, Asia and Australia, whereas *Pachycondyla* is neotropical.

lar behavior in *Tetramorium cespitum* and in some Camponotine ants of the genus *Lasius*. Hungry larvæ of *Aphenogaster* will even attack and devour smaller larvæ of their own species that lie within reach of their sharp mandibles.

Still the very young larvæ of *Aphenogaster* and possibly also

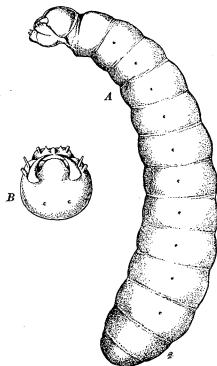


FIG. 3. A, nearly adult larva of *Megaponera farctens* Fabr.; B, head of same, dorsal view.

of the Ponerinæ are fed with liquid food regurgitated on their mouths by the workers. Miss Fielde thus describes the process in *Aphenogaster* (1901):

The feeding of the larva, which is bent nearly double in the egg, with regurgitated food begins as soon as it straightens itself and protrudes its mouth. When the larvæ begin to appear in the egg-packet, the workers lift the packet and hold it free and still, while one of their number holds a translucent white globule of regurgitated food to the larval mouth projecting from

the surface of the egg-packet. I have repeatedly seen the workers thus feeding the very young larvæ, a single globule of regurgitated food serving for a meal of which four or five larvæ successively partook.

Undoubtedly the majority of Myrmicinæ, Dolichoderinæ and Camponotinæ, the three most highly specialized subfamilies of ants, feed the brood throughout its larval stages with regurgitated liquids. Concerning larval feeding in the Dorylinæ nothing is known.

I come now to a consideration of some of the ant larvæ collected by Mr. Lang in the Belgian Congo. Four of these, all belonging to the subfamily Myrmicinæ, are of unusual interest. One of the species is a new *Pædalgus* which I shall describe elsewhere as *P. termitolestes* sp. nov., the third of the genus to come to light, as only one Indian and one other West African species were previously known. The workers of *termitolestes* are minute brownish yellow ants which live in the masonry of large termite hills and undoubtedly prey on their inhabitants. Their habits therefore resemble those of the well-known thief-ants, *Solenopsis molesta* of North America and *S. fugax* of Europe. The larva (Fig. 5) has a singular shape, being almost spherical, with a short neck, small head and minute, bidentate mandibles. The delicate integument is studded with very short, stiff hairs, each of which has two recurved branches. The larvæ, which are held together in compact masses by the interlocking of these hooked hairs, are fed with liquid food by regurgitation as is evident from the contents of their large spherical stomachs and the very feeble development of their mouthparts. Although, like other Myrmicinæ, they do not spin cocoons but form naked pupæ, they nevertheless possess huge salivary glands. Even in the very young larva (Fig. 5A) the salivary receptacle on each side is full of a clear liquid secreted by the large cells of the two branches of the gland. In the nearly full-grown female larva (Fig. 5B) the glands are very voluminous and have their lumen and that of the receptacle full of secretion shown as dark, compact masses in the figure, which was, of course, drawn from a specimen hardened and dehydrated in alcohol. As such an amount of saliva would hardly be necessary for digestive purposes and as it is not used in the form of silk by the full-grown larva, it probably serves as a store of food for the nurses. The *Pædalgus* larvæ, therefore, would

seem to resemble the repletes of honey ants (*Myrmecocystus*, *Leptomyrmex*, etc.), except that the food for the workers is metabolized and stored as saliva by the larva, instead of merely being ingurgi-

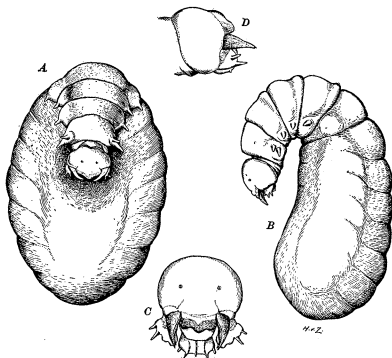


FIG. 4. Adult larva of *Bothroponera sublaevis* Mayr. A, ventral; B, lateral view; C, head, dorsal view; D, head, in profile.

tated and stored in the ingluvies, or crop by a certain number of workers. From the fact that other Myrmicine ants, although they spin no cocoons, often have well-developed salivary glands, we may infer that these organs have much the same function as in *Pædalagus*. To prove this, however, additional observations are necessary, though other reasons for believing it to be the case, will appear in the sequel. In all the larval stages of the Dolichoderinæ and in the immature larvæ of Camponotinæ the salivary glands are probably put to a similar use. In the species of *Æcophylla* and *Polyrhachis* that employ their young larvæ for spinning the silken portions of

the nest inhabited by the whole colony, we must suppose that the spinning habit, which in other Camponotine ants is manifested only at the end of larval life, has become secondarily precocious, but even in such larvæ the saliva in the stages immediately after hatching may, perhaps, still serve as an agreeable draught for the nurses.

The three remaining larvæ which I wish to describe belong to species formerly included in the genus *Sima* but now for taxonomic

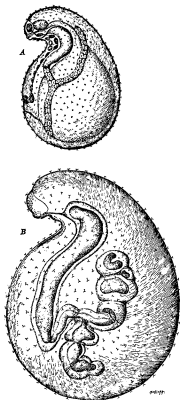


FIG. 5. *A*, very young; *B*, nearly adult larva of *Padalgus termitolestes* sp. nov.; lateral view to show the development of the salivary glands.

reasons referred to *Tetraponera* and *Pachysima*. These ants live in hollow twigs like the species of the closely related neotropical genus *Pseudomyrma*. A large collection of *Tetraponera tessmanni*, made by Mr. Lang, included larvæ and pupæ in all stages of de-

velopment. The adult larva differs little from the youngest and is shown in Fig. 6. It is long, cylindrical and hypocephalic, *i. e.*, with the head on the ventral side instead of being terminal. Unlike the various larvæ described above, it has a pair of swollen appendages, belonging to the prothoracic segment and applied to the sides of the

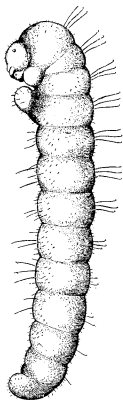


FIG. 6. Adult larva of *Tetraoponera tessmanni* Stitz.

head, and a large protuberance, evidently representing a pair of fused appendages, on the ventral side of the first abdominal segment. The dorsal surface is furnished with long, hook-shaped hairs, by means of which the larva is evidently suspended from the walls of the nest in the same manner as some of our American ant larvæ (*Pheidole*, *Leptothorax*, etc.) which have similar dorsal hairs.

Other larvæ of *Tetraponera* (*natalensis*, *allaborans*, etc.) are not unlike those of *T. tessmanni*.

The meaning of the thoracic and abdominal appendages becomes clear when we examine the larvæ of *Pachysima athiops* and *latifrons*. Four distinct stages, probably separated by moults, or ecdyses, may be recognized in *athiops*. The first stage larva, just after hatching, is represented in Fig. 7 as it appears in ventral and

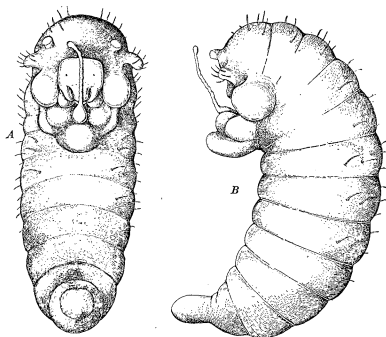


FIG. 7. First larva stage ("trophidium") of *Pachysima athiops* F. Smith. A, ventral; B, lateral view.

lateral view. The body is curved, convex dorsally and concave ventrally, and terminates behind in a cylindrical projection, with the anus shifted to the ventral surface near its base. The creature is strongly hypocephalic like the larval *Tetraponera* and *Pseudoponera*. The head is surrounded by a cluster of prominent, tubercle-like appendages. On the prothorax, which is large and forms a great hood over the head, there are three pairs of these appendages, an anterior truncate pair, a median pointed pair and a large posterior pair,

swollen and rounded and embracing the sides of the head. These evidently correspond to the single prothoracic pair of the *Tetraponera tessmanni* larva. The mesothoracic segment has a pair of smaller appendages nearer the mid-ventral line. Between them arises a very peculiar organ with a swollen, pear-shaped base prolonged into a slender, apparently erectile, tentacle-like process which extends up in front of the head and terminates in a small ampulla. The first abdominal segment bears a pair of large swollen appendages lying at the base of the mesothoracic pair and united with a large and very prominent mid-ventral tubercle. This tubercle and its lateral appendages are represented in the *T. tessmanni* larva but the others, with the exception of the third prothoracic pair, are absent. Sections and stained, cleared preparations of the whole larva show that the various tubercles contain portions of the fatbody, at least in the bases of their cavities, and next to the hypodermis a dense, granular substance, evidently a coagulated liquid produced by the underlying adipocytes, or trophocytes. The same liquid also fills the unpaired tentacle, except its pear-shaped base, which contains fat cells. Around the bases of the tubercles are muscles so arranged that their contraction must increase the pressure on the fat and granular liquid and in all probability cause the latter to exude through the hypodermis and delicate chitinous cuticle onto the surface. The whole arrangement of the tubercles, in fact, constitutes a system of exudate organs, or exudatoria, as I shall call them, adapted to secrete substances that can be licked up by the ants when they are feeding and caring for the larvæ. In this stage the mandibles are small, soft, blunt and unchitinized so that the larva must be fed with regurgitated liquid food. The labium has a peculiar pair of fleshy appendages, shown just beneath the mandibles in 7A. The body is naked, except for a few sparse, pointed bristles on the dorsal surface and the median pair of prothoracic appendages. As nothing like this larval stage is known among ants or indeed among the Hymenoptera, I propose to call it the "trophidium."

The second stage larva is shown in Fig. 8A. The various exudatoria are smaller in proportion to the remainder of the body but are still much like those of the trophidium. The body is more elliptical, the mandibles are more pointed and distinctly falcate, but even in

this stage they are unchitinized and therefore nonfunctional. The coarse hairs are visible on the dorsal surface but a more uniform investment of small hairs has made its appearance. They are blunt or even clavate, especially on the prothoracic segment. In this and the trophidium stage I am unable to find any salivary glands in cleared preparations though rudiments may, perhaps, be present.

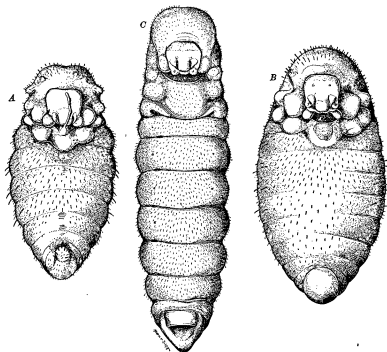


FIG. 8. A, second, B, third and C, fourth (adult) larval stages of *Pachysima ethiops* F. Smith.

The third stage larva (Fig. 8B) is larger and very regularly elliptical. The exudatoria can all be recognized, except the unpaired tentacle. It is, however, present in some of the younger individuals but in a greatly reduced and vestigial condition and at the bottom of the deep depression which now appears as a definite pocket just back of the mouth and under the midventral swelling of the first abdominal segment. In many larvæ I found in this pocket a small,

rounded, dark-colored pellet, which puzzled me at first. In sections, however, it was at once seen to consist of the triturated and compacted bodies and parts of small insects. It is, in fact, a food-pellet placed by the worker ants in the pocket just behind the larva's mouth. In this stage, therefore, the larva is fed on solid food and the strongly chitinized, acute and bidentate mandibles corroborate this statement. Slender salivary glands may also be detected, indicating that the substance of the food-pellet is subjected to extraintestinal digestion. The longer hairs on the dorsal integument have almost completely disappeared. The first pair of appendages on the prothorax has disappeared and the second pair is obsolescent.

In the fourth, or adult stage (Fig. 8C) the larva is more elongate and cylindrical and much more hypocephalic, the prothorax forming a great protuberance in front of the head. The exudatoria are still recognizable, with the exception of the first and second prothoracic pairs, which have disappeared entirely. The labial appendages are reduced. A food pellet was found in the postcephalic pocket in several of the larvæ of this stage but is not represented in the figure. The coarse hairs have disappeared from the integument, which is now uniformly covered with very short, delicate hairs, and the structure of the posterior end of the body is very different from that of the preceding stages.

We owe the only account of the *athiops* larva in the literature to Emery (1912). He describes what corresponds to my fourth stage larva very briefly and figures its anterior end with some of the exudatoria, but erroneously interprets the large prothoracic pair as "ébauches de pattes," or rudiments of the anterior pair of imaginal legs.⁴

The larvæ of *Pachysima latifrons* are quite as extraordinary as those of *athiops* and also pass through four stages. The trophidium, or first stage, shown in Fig. 9, is very hypocephalic, the pro-

⁴ In the same paper Emery created the subgenus *Pachysima* for the accommodation of what was formerly called *Sima athiops* and for a new species described as *latifrons*, because they have the frontal carinæ of the worker and female much more widely separated than in the numerous species of *Tetraponera* (*Sima auctorum*). I have raised *Pachysima* to generic rank, because the larvæ of the two species are so very different from those of *Tetraponera*.

thoracic segment being greatly enlarged and projecting anteriorly. Both preparations stained *in toto* and sections, show that the portion of the fat-body in this segment is sometimes heavily charged with urate crystals, so that it undoubtedly functions as a storage kidney till the Malpighian vessels are sufficiently developed to excrete. The first and second pairs of prothoracic appendages of the *æthiops* larva are absent, but the third pair is very large and embraces the sides of the head. The meso- and metathoracic segments each bear a pair of slender pointed appendages, the first abdominal segment a

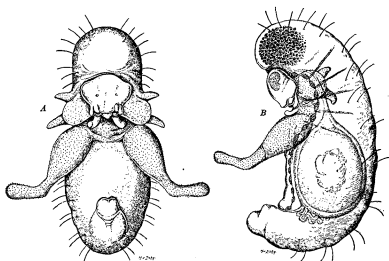


FIG. 9. First larval stage ("trophidium") of *Pachysima latifrons* Emery.
A, ventral; B, lateral view.

huge leg-like pair, which are swollen and fusiform at the base and run out into a long slender process which forms an obtuse angle with the basal portion. The sternal region between these appendages is protuberant and its cuticular covering, like that of the four pairs of appendages is minutely prickly, unlike the smooth cuticle of the remainder of the body. Sections show that both the appendages and the sternal swelling are exudate organs, though the prothoracic and abdominal pairs are much more important than the others. The prothoracic appendages are filled with blood and very

little fat tissue, but their hypodermis is much thickened and consists of crowded cells arranged in peculiar clusters. In section the abdominal appendages appear as in Fig. 10. The fusiform base is filled with large, clear trophocytes, or fat-cells, some of which in the middle of the swelling may contain urate crystals, like those in the prothoracic storage kidney, but the slender, tubular distal portion contains a granular liquid, which can only be regarded as an exudate

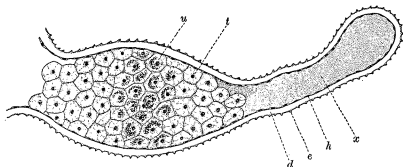


FIG. 10. Longitudinal section through exudatorium of first abdominal segment of trophidium of *Pachysima latifrons* Emery.

derived from the trophocytes in the basal enlargement. This exudate is evidently filtered through the thin cuticula covering the appendage by pressure, for there is a rather elaborate system of muscles, as in the *æthiops* larva, surrounding the bases of the appendages and capable of subjecting their contents to pressure. The head is small and has soft, blunt, rudimentary and unchitinized mandibles, and the labium bears a pair of long, palp-like appendages, which project forward in the deep depression between the head and the swollen sternal portion of the first abdominal segment. These are probably also exudatoria and seem roughly to correspond to the unpaired tentacle of the *æthiops* larva. The structure of the mouth-parts shows that the larva in this stage is fed with liquid food regurgitated by the workers. The convex dorsal surface is beset with sparse, curved bristles of uniform thickness, with blunt tips. The segmentation of the body is indistinct and its posterior end curves forward and terminates in a large tubercle with the anal orifice just anterior to its base. Fig. 9B, drawn from a stained and cleared

preparation, shows the nervous system and alimentary canal. The Malphigian vessels have only just begun to develop at the blind end of the proctenteron where it abuts on the posterior end of the large, elliptical mesenteron, or stomach, but no salivary glands can be detected.

In the second stage larva (Fig. 11*A*) the body is more elongate and cylindrical and the four pairs of appendages can still be recog-

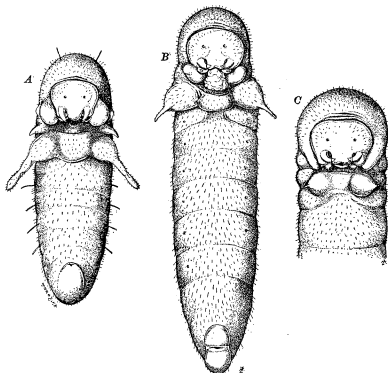


FIG. 11. *A*, second, *B*, third and *C*, fourth (adult) larval stages of *Pachysima latifrons* Emery.

nized though considerably smaller in proportion to the remainder of the body. The mandibles are becoming chitinized. Many of the long hairs on the dorsal surface are still present but a general covering of short, sparse hairs has made its appearance.

The third stage larva (Fig. 11*B*) is larger and still more elongate

and cylindrical and shows a further regressive development of the exudatoria. Those on the meso- and metathoracic segments have disappeared and the abdominal pair has short broad bases with the distal portions attenuated to slender points. The labial appendages have also disappeared. The mandibles are well chitinized and the larva is now fed with pellets of crushed insects, like the *æthiops* larva in the corresponding stage. These pellets were found *in situ* in several of the alcoholic specimens as represented in Fig. 11B. The pellet lies in the deep pocket between the head and the sternal protuberance of the first abdominal segment and is therefore within easy reach of the mandibles and labium of the larva. Cleared preparations show that the salivary glands have made their appearance, though they are small and slender.

The anterior end of the fourth stage, or adult larva is shown in Fig. 11C. The exudatoria of the prothoracic segment now appear merely as a pair of welts or folds embracing the sides of the head and continuous with the more dorsal portions of their segment, which is relatively smaller and less projecting than in the preceding stages. The exudatoria of the first abdominal segment are still distinct but their distal portions are reduced to mere points, sometimes absent in larvæ just before pupation, and the sternal swelling is much less prominent. In this stage the larva resembles that of *Tetraponera* throughout its various stages. In the third and fourth stages of the *latifrons* larva, as in the corresponding stages of *æthiops*, the salivary glands probably furnish secretions which are useful both in the extraintestinal digestion of the food pellet and as substances that can be imbibed by the workers. The fact that in the two species of *Pachysima* the exudatoria decline *pari passu* with the development of the salivary glands certainly suggests that both sets of organs have to some extent a common function. In forms like *Pædalagus* and probably many other Myrmicinae, in which the development of the salivary glands is more precocious, the exudatoria are not developed.

I believe, therefore, that we must interpret the exudatoria as very primitive glands, but they differ so much from the ordinary hypodermal glands of insects that it will be necessary to consider them more closely before proceeding further. They are, as we have seen, small

diverticula like the embryonic legs, consisting of hypodermis and its overlying cuticula and containing a portion of the fat-body separated from the hypodermis by a granular liquid.⁵ Now the fat-body of insects may be regarded as a diffuse ductless gland, the cells (trophocytes) of which take certain substances from the blood in which they lie, store them in the cytoplasm as fat-globules or proteid granules and later return them to the blood in a more finely divided, if not chemically modified form. The exudate which accumulates in the distal ends of the exudatoria is therefore merely blood charged with nutrient substances from the fat-cells, and either filters gradually through the hypodermis and overlying cuticle or is forced through them by muscular pressure. At first sight it would seem that the cuticle must be impervious to such a liquid, but a consideration of the more recent work on the minute structure of chitin by Holmgren (1901, 1902), Biedermann (1902, 1903), Kapzov (1911), Casper (1913) and others shows that there is nothing to prevent the passage of a thin fatty liquid, even if it were not under pressure and even if the cuticle were much thicker than it is in the ant larva. The cuticle is a colloid, either of a reticular structure, as Kapzov believes, or formed of horizontal layers of very fine fibrillæ crossing one another at an angle of 60° as most investigators, including Biedermann and Casper, maintain. Between the fibrillæ are regularly distributed and extremely fine openings or "pore canals," through which a liquid might readily pass as if the cuticle were a

⁵ The question arises as to whether the larval exudatoria of *Pachysima* are the homologues of the true appendages on the thoracic and first abdominal segments of embryo insects. In other words, do the exudatoria represent true legs or are they new formations? The trophidium of *P. latifrons* seems to point to the former alternative. The large leg-like exudatoria on the first abdominal segment are certainly very suggestive of the embryonic "pleuropodia" to which I devoted a paper many years ago (1890). On the other hand, the four pairs of trophidium appendages in *latifrons* seem to be homologous with the four pairs of papillæ in the larva of *Bothroponera* (Fig. 4), and the latter are almost certainly merely remnants of a considerable number of similar papillæ which are scattered over the whole surface of the larval *Pachycondyla*, *Diacamma* and *Ponera*. Furthermore, two of the pairs of exudatoria on the prothorax of the *Pachysima ethiops* trophidium and the unpaired tentacle-like exudatorium just behind the head cannot be brought into the homology. It would seem, therefore, that the exudatoria must be regarded as cœnogenetic, or new formations peculiar to the young larvæ of certain Old World genera of Pseudomyrmini.

filter. Even in the case of the hypodermal glands fatty liquids are known to pass through the thin chitinous cuticle with which the secreting surface of the cytoplasm is always covered, even where the ends of the ducts are intracellular.

In this connection attention may be called to a very similar exudation of blood plasma charged with certain substances (*e. g.*, cantharidin) through the hypodermis and cuticle in many Meloid, Cantharid, Lampyrid, Coccinellid and Chrysomelid beetles. It has long been known that when these insects are roughly handled they discharge from the articulations of their legs a white, yellow or greenish, bad-smelling liquid, which Magretti (1881, 1882), Lutz (1895), De Bono (1889) and Berlese (1909) have shown to be blood plasma. It accumulates in pockets at the articulations after passing through the integument and leaving the blood cells (amœbocytes) behind, and is clearly an exudate though it is repugnatorial instead of having an alluring or nutrient function like the blood plasma of *Pachysima*.

It is unnecessary, however, to seek confirmation of my interpretation of the circumoral appendages of the *Pachysima* larva by merely pointing to the conditions in the Meloids, Coccinellids, etc. Wasmann, Holmgren and Trägårdh have published valuable studies of exudate organs much more like those of the ant larvæ. To Wasmann (1903) belongs the credit of having first made an extensive investigation of the trichome glands and exudatoria of numerous myrmecophiles and termitophiles. Many of these structures are more or less modified hypodermal glands with tenuous ducts opening at the base of hairs (trichomes) which either diffuse the secretion so that it can evaporate quickly or spread it out so that it can be readily licked up by the ants, but in such termitophiles as the Staphylinid beetle *Xenogaster inflata*, the fat-body in certain parts of the abdomen forms "blood tissue," which becomes the "exudate" by passing through a layer of hypodermis at the base of papillæ ("exudate buds").⁶ The latter seem to consist of cuticular substance perforated by delicate canals that conduct the exudate to the surface. Wasman says:

The exudate of these buds seems therefore to be a component of the blood fluid, which is as it were filtered through the hypodermal layer.

⁶ The trichome glands may be compared with similar structures in other

Some of the details in his account and figures are far from clear, but there can be no doubt about his meaning. Equally interesting is his description of the larvæ of certain symphilic myrmecophiles (*Lomechusa*, *Atemeles* and *Xenodusa*) concerning which he writes:

The cuticula of the whole body, excepting the head, is membranous and whitish. Outer exudate organs (*i. e.*, trichomes) are lacking. The exudate tissue is exclusively the fat-body.

He believes, in other words, that in these larvæ the voluminous fat-body functions as a huge exudatorium which pours a fatty exudate onto the surface of the body. This at once suggests that in many ant larvæ the general fat-body may have the same function, so that there would be in these insects three possible sources of liquid substances agreeable to the worker ants. the salivary glands, the exudatoria *sensu stricto* and the fat-body. They would not all be equally developed in any given species, but at any rate there is just as much reason for supposing that the general fat-body may function as an exudate organ in the ant-larva as in the larvæ of the *Lomechusine* myrmecophiles. Krüger (1910) and Jordan (1913) have cleared up some of the obscurities in Wasmann's paper, especially in regard to the trichome glands of hypodermal origin, but in my opinion have not invalidated his general conclusions in regard to the role of the fat-body and blood in exudation.⁷

animals. Many nonmyrmecophilous insects have similar glands that serve to diffuse sexually attractive secretions. The question arises as to whether many of the hair-tufts in mammals may not have an analogous function. Anthropologists seem not to have explained the retention of hairs in the axillary and pubic regions of man. It is evident that the hairs in the armpits serve rapidly to diffuse and evaporate the secretions of the sudorific glands. The pits full of trichomes on the thorax of many symphilic Paussid beetles are strangely suggestive in this connection. The function of the public hairs is not so clear, but perhaps certain bats which have peculiar tufts about the genitalia (see, *e. g.*, the figures of the Congolese *Hipposideros langi* Allen in *Bull. Amer. Mus. Nat. Hist.*, 37, 1917, pp. 436, 437) may indicate that in the remote past the public hairs had a sexual function in the ancestors of man.

⁷ For a critique of Jordan's work and for further discussion of the structure and development of *Lomechusa* and *Atemeles* the reader is referred to Wasmann's recent monograph: "Neue Beiträge zur Biologie von *Lomechusa* und *Atemeles*" (1915).

Wasmann has shown in a number of papers that the true guests of termites, the symphiles, are physogastric, *i. e.*, have the abdomen enormously distended with fatty tissue. This condition is very striking in certain Staphylinids (*Xenogaster*, *Corotoca*, *Spirachtha*, *Termitomimus*, etc.) and Diptera (*Timeparthenus*, *Termitomyia*, *Termitoxenia*, *Thaumatoxena*, etc.). Trägårdh (1907) has studied sections of the beetle *Termitomimus*, which lives in considerable numbers in the *Eutermes* colonies of Zululand. His description of the exudate organs is so much clearer than Wasmann's and so significant in connection with my account of the *Pachysima* larvæ, that I quote the greater part of it:

The relation of the fat-body to the hypodermis and the cuticle is different in different parts of the body.

1. The hypodermis is exceedingly thin, sometimes scarcely discernible and pressed close to the cuticle by the underlying fat-body. The cuticle has no distinct endostracum and is penetrated by an immense number of extremely fine pores, arranged in transverse rows. This is the case with the ventral, lateral and posterior part of the pseudoabdomen, *i. e.*, exactly where the cuticle is of a bright reddish-yellow color ("symphilous color" Wasmann) and where the termites may most easily get access to it.

2. The hypodermis is thick and withdrawn from the cuticle which is thicker, with well-developed epiostracum and endostracum, leaving a rather wide space, which is filled with liquid. . . . The fat-body is contiguous to the hypodermis. The space between the cuticle and the hypodermis is more or less filled with a cyanophilous tissue of a spongy appearance which sometimes exhibits a very distinct radial structure, sometimes is concentrically stratified and contains numerous granules which are also to be found in the trichogenic cells. This is evidently a fluid, which has either passed through the hypodermis and is a derivative from the fat-body or it is a secretion produced by the hypodermis and is coagulated by the method of fixation. . . .

The above stated facts concerning the relation of the fat-body to the hypodermis and the cuticle differ in some essential respects from what Wasmann has found in the termitophilous physogastrous insects studied by him. In *Spirachtha*, *Termitoxenia*, the larvæ of *Orthogonius* and *Glyptus*, in *Xenogaster* and other Aleocharini the hypertrophied fat-body is always surrounded by large tracts of blood-tissue, consequently the exudation is derived directly from the blood-tissue and only indirectly from the fat-body. The exudation is no fluid but evaporates through the membranous cuticle, which has no pores.

To support the theory of the exudation being only an attractive odor and not offering the termites any source of subsistence Wasmann points out the fact that the symphili as a rule only occur in small numbers in the nests.

These statements, however true they may be with regard to the above mentioned genera, do not apply at all to *Termitomimus*. In this genus on the

contrary, in the part of the abdomen which is easiest accessible to the termites, viz., the ventral, lateral and posterior side of the pseudoabdomen,

1. The fat-body is not surrounded by the blood-tissue but contiguous with the extremely thin hypodermis and

2. The cuticle is penetrated by an immense number of pores (and the endostracum is not distinctly discernible).

3. Furthermore *Termitomimus* does occur in great numbers in the nests of the termites.

These facts seem to me to suggest that in *Termitomimus* the fat itself or a derivate of the fat-body may possibly be secreted as a fluid through the numerous pores of the cuticle and not merely evaporate and that *Termitomimus* thus offers to the termites a source of subsistence. The comparatively very large extension of the area of the cuticle which exhibits this structure also argues in favor of this theory.

In another paper (1907a) Trägårdh describes a peculiar Tineid caterpillar with exudatoria even more like those of the *Pachysima* larva. He found it in the tree nests of *Rhinotermes* in Zululand. The relations between the caterpillar, which feeds on the woody substance of the nest, and the termites are evidently friendly.

When disturbed, the larvæ were seen to make their way to other parts of the nest, coming along one after the other, with regular intervals, like in a procession, each larva being escorted by a few soldiers and workers.

Each of the seven anterior abdominal segments of the caterpillar bears on its sides a pair of long, tapering appendages, which Trägårdh regards as exudatoria and each appendage contains a lobe of the fat-body, surrounded by blood. The imperforate hypodermis is separated from the thin cuticle, the space between being filled with exudate. In this case he believes that the exudate must evaporate on the surface of the body, since he says:

As the larva emits a strong odor, and the termites were scarcely seen touching the appendages, the exudation is very likely an alluring odor.

He compares the organs with the various osmateria described by Packard in the caterpillars of *Megalopyge* and *Hemileucidæ*.

Certain organs in the larvæ of two groups of Hymenoptera may also be interpreted as exudatoria. In 1907 I called attention to peculiar blister-like organs on the sides of pseudonymphs of certain Eucharine parasites of ants, notably in *Orasema*. These structures are shown in Figs. 19 and 21, Pl. 2 of the paper referred to and in Fig. 251 F, G, p. 415 of my ant book (1910). In the pupa of the

same insect the abdomen has similar organs in the form of transverse welts. Reichensperger (1913, Pl. 6, Fig. 12) describes and figures the very same organs in an Abyssinian Eucharine, *Psilogaster fraudulenta*, which lives with *Pheidole megacephala*, and suggests that they may be exudate organs. Forel (1890) had previously mentioned similar structures ("asperités et boussoufflures") on the pupa of the large *Eucharis myrmeciae* taken from the cocoon of an Australian bulldog ant, *Myrmecia forficata*. On recently reexamining my preparations I find that the organs of *Orasema viridis* may be interpreted as exudatoria. They are knob-shaped, with very thin hypodermis and cuticle and are filled with blood but contain no fat-tissue, although the fat-body in the abdomen and thorax is very voluminous. In life the knobs are colorless and glistening. Both the pseudonymphs and pupæ are assiduously licked by their host, *Pheidole instabilis*, so that the knobs of the former and the welts of the latter probably produce substances agreeable to the ants.⁸

The other group of Hymenoptera comprises the singular South African bees of the genus *Allodape*. In 1902 Brauns showed that they make very primitive nests, consisting of a single cavity, often 12 cm. long, in the stems of various Liliaceous plants, but unlike all other solitary bees, feed their larvæ from day to day with "Futterbrei" (honey-soaked pollen?). In the warmer portions of Cape Colony and German Southwest Africa *Allodape* breeds throughout the year. The single cavity of the nest contains eggs, larvæ in all stages, pupæ and freshly emerged bees intermingled. The larvæ are unique among bees in possessing peculiar tubercles on the sides of the fifth to tenth segments. Friese (1914) publishes photographs of some rather shrivelled half-grown larvæ and describes the tubercles as "bladderlike evaginations of the outer skin." Brauns seems to regard them as legs (pseudopods) and says that they are used to hold the food, but it seems probable that they are really

⁸ While this paper was in the hands of the printer Dr. R. J. Tillyard of New South Wales sent me the larvæ, pupæ and an adult male of a huge undescribed Eucharine, which he found attacking the brood of the red bulldog ant (*Myrmecia gulosa*). Prof. C. T. Brues believes that the parasite may belong to the genus *Psilogaster* and will describe it in the near future. The larvæ and pupæ are covered with exudatoria like those of *Orasema* but more prominently developed.

exudate organs. If this proves to be true, the resemblance of *Allo-dape* to *Pachysima*, which also rears its brood in all stages in hollow stems and feeds the older larvæ with food-pellets, would be very striking. *Allodape* is also of considerable interest in connection with Roubaud's observations on the wasp *Synagris* which will be considered in the sequel.

More important in their bearing on the exudate organs of *Pachysima* are Holmgren's observations on the termites. He devotes the twelfth chapter of his volume (1909) on the anatomy of these insects to the exudate tissue. Termites are really themselves physogastric like their guests, and Holmgren shows that all the castes, but especially the queens, have extensive exudate tissues, consisting of the peripheral layers of the abdominal fat-body. In these layers the trophocytes do not contain fat-globules but numerous minute granules which are discharged into the blood and thus convert it into the exudate that passes through numerous pores or lacunæ in the chitinous cuticle to the surface. There it is licked up by other members of the colony. He finds that the development of the exudate tissue differs considerably not only in the different castes but also in their various developmental stages and

that the intensity of the licking and feeding of the individuals of a termite colony is directly proportional to the amount of their exudate tissue. Those with the largest mass of exudate tissue are the best fed and the most licked. In other words, the care bestowed by the workers on the various members of the colony is not an immediate expression of an altruistic philoprogenitive instinct (*Brutpflegeinstinct*), but depends essentially on egoistic motives, *i. e.*, exudate hunger.

To this point I willingly follow Holmgren, but both he and Wasmann have used their respective observations as a basis for what seem to me to be rather dubious speculations, a consideration of which will have to be deferred till the more general part of my discussion is reached.

Escherich (1911) gives a more vivid, not to say more spectacular account of the exudate hunger of termites. So eager are the workers of the Ceylonese *Termes redemanni* for the exudate of their huge physogastric queen that they actually tear little strips out of her cuticle in order to get at the liquid more readily! Escherich found that old queens sometimes have their white ab-

domens dotted with the small brown scars of the wounds thus inflicted by their progeny. Here the feeding behavior of the mother and offspring is the reverse of that in incipient ant colonies, since the queens are fed with regurgitated food by the workers and feed the latter with exudates, but this is, in all probability, also the case in established ant colonies when the workers have matured and the queen no longer feeds the brood.

The facts collated in the foregoing paragraphs relate to the exudate organs, but we had previously seen that the salivary glands of larval ants probably subserve a similar function in the life of the colony in addition to digesting proteid foods extraintestinally and producing silk at the time of pupation. The question arises as to whether there is any evidence that in other groups of social insects the salivary glands of the larva produce substances which are consumed by the worker nurses. Fortunately there are some very pertinent observations at hand in the French literature which is so rich in splendidly original works on the habits and taxonomy of insects. The observations to which I refer relate to the social wasps. Du Buysson (1903) observed that the larvæ of *Vespa* "secrete from the mouth an abundant liquid. When they are touched the liquid is seen to trickle out. The queen, the workers and the males are very eager for this secretion. They know how to excite the offspring in such a way as to make them furnish the beverage." And Janet (1903) was able to prove that the secretion is a product of the salivary, or spinning glands and that it flows from an opening at the base of the labium. "This product," he says, "is often imbibed by the imagines, especially by the just emerged workers and by the males, which in order to obtain it, gently bite the head of the larva."

The most illuminating study of this matter, however, is found in a fine paper by Roubaud on the wasps of Africa (1916). His account of the primitive wasps of the genus *Belonogaster* presents a striking picture of one of the earliest stages in the social life of wasps, as will be seen from the following quotation:

In the species of *Belonogaster* as well as in those of the genera *Icaria* and *Polistes* we have been able to observe this proceeding in detail. All the larvæ, from birth, secrete from a projection of the hypopharynx, on the inferior surface of the buccal funnel, an abundant salivary liquid, which at the slightest touch spreads over the mouth in a drop. All the adult wasps,

males as well as females, are extremely eager for this salivary secretion, the taste of which is slightly sugary. It is easy to observe, especially in *Belonogaster*, the insistent demand for this larval product and the tactics employed to provoke its secretion.

As soon as a nurse wasp has distributed her food pellet among the various larvæ, she advances with rapidly vibrating wings to the opening of each cell containing a larva in order to imbibe the salivary drop that flows abundantly from its mouth. The method employed to elicit the secretion is very easily observed. The wing vibrations of the nurse serve as a signal to the larva, which, in order to receive the food, protrudes its head from the orifice of the cell. This simple movement is often accompanied by an immediate flow of saliva. But if the secretion does not appear the wasp seizes the larva's head in her mandibles, draws it towards her and then suddenly jams it back into the cell, into which she then thrusts her head. These movements, involving as they do a stimulation of the borders of the mouth of the larva, compel it to secrete its salivary liquid.

One may see the females pass back and forth three or four times in front of a lot of larvæ to which they have given nutriment, in order to imbibe the secretion. The insistence with which they perform this operation is such that there is a flagrant disproportion between the quantity of nourishment distributed among the larvæ by the females and that of the salivary liquid which they receive in return. There is therefore a real exploitation of the larvæ by the nurses.

The salivary secretion may even be demanded from the larva without a compensatory gift of nourishment, both by the females that have just hatched and by the males during their sojourn in the nest. The latter employ the same tactics as the females in compelling the larvæ to yield their secretion. They demand it especially after they have malaxated an alimentary pellet for themselves, so that there is then no reciprocal exchange of nutritive material.

It is easy to provoke the buccal secretion of the larvæ artificially. Merely touching the borders of the mouth will bring it about. The forward movement of the larvæ at the cell entrance, causing them to protrude their mouths to receive the food pellet, is also easily induced by vibrations of the air in the neighborhood of the nest. It is only necessary to whistle loudly or emit shrill sounds near a nest of *Belonogaster* to see all the larvæ protrude their heads to the orifice of the cells. Now it is precisely the vibrations of the air created by the rapid agitation of the bodies of the wasps and repeated beating of their wings that call forth these movements, either at the moment when food is brought or for the purpose of obtaining the buccal secretion which is so eagerly solicited.

Roubaud summarizes the general bearing of his observations in the following paragraph:

The reciprocal exchange of nutriment between the adult females and the larvæ, the direct exploitation of the larval secretion without alimentary compensation by the males and just emerged females are trophobiotic phenomena the elucidation of which is of great importance to an understanding of the

origin of the social tendencies in the Vespidae, as we shall show in the sequel. The retention of the young females in the nest, the associations between isolated females, and the coöperative rearing of a great number of larvæ are all rationally explained, in our opinion, by the attachment of the wasps to the larval secretion. The name *œcotrophobiosis* (from *oikos*, family) may be given to this peculiar family symbiosis which is characterized by reciprocal exchanges of nutriment between larvæ and parents, and is the *raison d'être* of the colonies of the social wasps. The associations of the higher Vespids has, in our opinion, as its first cause the trophic exploitation of the larvæ by the adults. This is, however, merely a particular case of the *trophobiosis* of which the social insects, particularly the ants that cultivate aphids and coccids, furnish so many examples.

It does not seem to me that the term "*œcotrophobiosis*" is aptly chosen. Apart from its length, it implies, as Roubaud states, a relationship between adult and larval members of the same colony or family, comparable with that existing between ants on the one hand and Aphids, Coccids, Membracids and Lycænid larvæ on the other. This relationship, however, is, so far as nutrition is concerned, one-sided since the ants exploit the aphids, etc., and may defend or even transport them, but do not feed them. Moreover, even in *Belonogaster* the feeding of adults and larvæ is reciprocal, and the latter could not be reared if they were actually exploited to such an extent as to interfere with their growth. As the relationship is clearly coöperative or mutualistic, I suggest the term *trophallaxis* (from *τροφή*, nourishment and *ἀλλάττω*, to exchange) as less awkward and more appropriate than "*œcotrophobiosis*."

That the feeding of the young by the mother wasp without compensation is more primitive than the condition in *Belonogaster* is shown by Roubaud's beautiful observations (1908, 1910, and 1916) on three species of *Synagris* in the Belgian Congo (*callida*, *sicheliana* and *cornuta*). These wasps represent important stages in the transition from the solitary to the social forms, since they make earthen cells like other Eumenids, lay eggs in them and provide the young with paralyzed caterpillars of Hesperid butterflies. In favorable seasons, when caterpillars are bundant, the behavior is like that of our northern Eumenid and Odynerid wasps, numerous small or single large caterpillars being placed with the egg in the cell and the latter sealed up ("approvisionnement massif accéléré"), but when the season is less unfavorable and food scarcer, the wasp's ac-

tivities slow down so that the larva may hatch before all the prey is brought in ("approvisionnement massif ralenti"). This condition leads naturally to a feeding of the larva from day to day with living but paralyzed caterpillars ("éducation surveillée indirecte") and eventually to a stage essentially like that of the social wasps in which the caterpillar is chewed up and placed as a pellet in the mouth of the larva ("éducation surveillée directe"). *Synagris cornuta* has reached this last stage. The mother insect, while malaxating the caterpillar, herself imbibes its juices.

The internal liquids having partly disappeared during this process of malaxation, the prey is no longer, as it was in the beginning, soft and juicy and full of nutriment for the larva. It is possible, in fact, to observe that the caterpillar *patée* provided by the *Synagris cornuta* is a coarse paste which has partly lost its liquid constituents. There is no exaggeration in stating that such food would induce in larvæ thus nourished an increase of the salivary secretion in order to compensate for the absence of the liquid in the prey and facilitate its digestion.

It is here that the further development to the condition seen in *Belonogaster* and other social wasps sets in. The mother wasp finds the saliva of the larva agreeable and a trophallactic relationship is established. As Roubaud says,

the nursing instinct having evolved in the manner here described in the Eumenids, the wasps acquire contact with the buccal secretion of the larva, become acquainted with it and seek to provoke it. Thence naturally follows a tendency to increase the number of larvæ to be reared simultaneously in order at the same time to satisfy the urgency of oviposition and to profit by the greater abundance of the secretion of the larvæ.

Although considerable evidence thus points to trophallaxis as the source of the social habit in wasps, ants and termites, it must be admitted that the phenomenon has not been observed in the social bees. That the latter may have passed through a phylogenetic stage like that of *Synagris* seems to be indicated by the solitary bees of the genus *Allodape* to which I have already referred (p. 318). Brauns' observations, though meager, show nevertheless that *Allodape* has reached Roubaud's fourth stage, that of direct feeding of the larvæ from day to day, and if I am right in supposing that the peculiar appendages of the larvæ are exudate organs, there would be grounds for assuming that trophallaxis occurs in this case. On

the other hand, it has often been suggested (*e. g.*, by von Buttel-Reepen) that the three social subfamilies, the stingless bees (*Meliponinæ*), bumble-bees (*Bombinæ*) and honey bees (*Apinæ*) have developed from the solitary bees by another and more direct path, for the *Meliponinæ*, though living in populous societies, still bring up their brood in essentially the same way as the solitary bees, *i. e.*, by sealing up the eggs in cells provisioned with honey-soaked pollen. The *Bombinæ*, however, keep opening the cells from time to time and giving the larvæ a little food at a time, and in the honey bee the cells are left open till pupation and the larvæ fed more continuously. Numerous facts indicate that the *Bombinæ* are the most primitive, the *Apinæ* the most specialized of existing social bees, and that the *Meliponinæ*, though closely resembling the solitary bees in the care of the young, are nevertheless in other respects very highly specialized (vestigial sting, elaborate nest architecture, etc.). It is therefore not improbable that these bees, after passing through a stage more like that of the *Bombinæ*, have reverted secondarily to a more ancient method of caring for their brood. At any rate, the *Meliponinæ* have been so little studied, as compared with the *Bombinæ* and *Apinæ*, that they can be left out of the present discussion. Sladen (1912) has given us a good account of the queen bumble bee feeding the larvæ, but he says nothing about the salivary glands of the latter. These are very large, as we know from the work of Bordas (1894), but their development is perhaps fully accounted for by the complete cocoon spun by the mature larva. Even in the honey bee, which has been so thoroughly studied, I find no evidence that the adult workers feed on larval secretions. In both cases, however, it is impossible under natural conditions accurately to observe the behavior of the larva while it is being fed. This might, perhaps, be done if the bees could be induced to rear their young in glass tubes made to resemble the cells.⁹ But even if it should be found, on further investigation, that there is no indication of reciprocal feeding between the larval and adult *Bombinæ* and *Apinæ*, we might still contend that these very highly specialized

⁹ Dr. E. F. Phillips informs me that it would be possible to observe the behavior of honey-bee larvæ and their nurses in cells built against and partly formed by the glass wall of an observation hive.

insects had in their evolution passed far beyond the stages represented by the termites, ants and social wasps. There can, indeed, be little doubt that the bees are descended from wasp-like ancestors and that they must therefore have passed from an animal to a vegetable diet. If the change of diet took place after the social habit had been established, as is possible and as is so clearly shown to be the case in the harvesting and fungus-growing ants, the loss of a resort to the larval secretions by the adult social bees could be readily explained as due to the abandonment of a scarce animal food, procured with considerable difficulty, for nectar and pollen, which are abundant and easily obtained.

Another objection that may be urged against the view that trophallaxis is so fundamental as I contend, is the behavior of the ants towards their inert pupæ, which though transported and defended as assiduously as the larvæ, yield neither liquid exudates nor secretions. This does not seem to me to be a serious objection, because the pupæ evidently have an attractive odor and may therefore be said to produce volatile exudates like certain myrmecophiles. Both the larvæ and pupæ, moreover, evidently represent so much potential or stored nutriment available for the adult ants when the food-supply in the environment of the colony runs very low or ceases entirely. Infanticide and cannibalism then set in with the result that the devouring of the young of all stages may keep the adult personnel of the colony alive till the trophic conditions of the environment improve. Certain predatory tropical species (*Dorylinæ*, *Cerapachyini*) regularly raid the colonies of other ants and carry home and devour their brood. In northern Eurasia and North America *Formica sanguinea* makes similar raids on colonies of *Formica fusca* but permits a certain number of the pupæ to hatch and become "slaves." The latter, however, represent only a small portion of the pupæ secured during the course of the summer. Wasmann believes that the *fusca* pupæ are plundered for the sake of being reared. This I doubt, but if true, we should have to account for it by supposing that to the *sanguinea* workers the odor of the *fusca* pupæ is, if anything, even more attractive than that of their own.

If we confine our attention largely to the ants, I believe it can

be shown that trophallaxis, originally developed as a mutual trophic relation between the mother insect and her larval brood, has expanded with the growth of the colony like an ever-widening vortex till it involves, first, all the adults as well as the brood and therefore the entire colony; second, a great number of species of alien insects that have managed to get a foothold in the nest as scavengers, *i. e.*, other species of ants (social parasitism); fourth, alien insects gers, prædators or parasites (symphily); third, alien social insects, that live outside the nest and are "milked" by the ants (trophobiosis), and, fifth, certain plants which are visited or sometimes partly inhabited by the ants (phytophily). In other words the ants, have drawn their living environment, so far as this was possible, into a trophic relationship, which, though imperfect or one-sided in the cases of trophobiosis and photophily, has nevertheless some of the peculiarities of trophallaxis. A brief sketch of each of these five expansions, indicated as annular areas in the accompanying diagram (Fig. 12), may not be out of place.

1. There is a very close resemblance between the behavior of adult ants towards one another and their behavior towards their young. The adults feed one another with regurgitated food or even with secretions as is the case with *Crematogaster (Physocrema) inflata*, an Indomalayan species, the workers of which have great sugar-glands in the back of the thorax. Many ants transport each other, and the transported ant assumes a quiescent, larval or pupal attitude. This is best seen in certain Ponerinæ, *e. g.*, in the species of *Lobopelta*, which carry their males under the body as if they were larvæ or pupæ. On such occasions the males keep their legs and antennæ in the pupal position. Moreover, when the food-supply of the colony is cut off ants often devour other ants of the colony as if they were larvæ or pupæ. The largest workers (soldiers) are eliminated first, either because they represent more stored food or because their continued life in the colony constitutes a greater drain on the food resources, or for both reasons. Some years ago I recorded an instance of this behavior in an Arizona ant, which I called *Pheidole militicida*, because it regularly kills and eats all the large-headed soldiers in the colony during the winter when the food supply is very limited. In artificial nests of *Camponotus*, which has poly-

morphic workers, a similar elimination of the largest individuals may be observed when the colony is left long without food.

2. Among myrmecophiles and termitophiles Wasmann has shown that there are certain species (symphiles) that have trophallactic re-

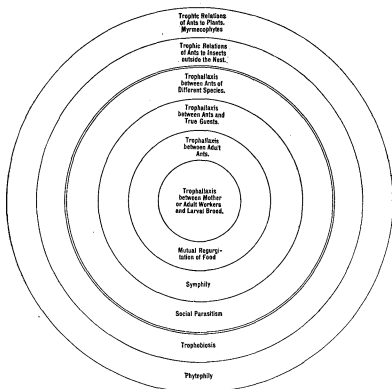


FIG. 12 Diagram to illustrate the expansions of the trophallactic and trophic relationships within and outside the ant colony. The confines of the nest are indicated by the double line.

lations with their hosts. Among ants especially these relations are so intimate that the symphiles may be regarded as integral members of the colony. The adult Lomeschusine beetles, *e. g.*, are not only fed and licked, but their young are treated as if they were ant larvæ, owing to the presence of trichome glands ("external exudate organs" of Wasmann) in the former and fatty, or internal exudatoria in the latter.

3. The various parasitic ants, of which a number of species have come to light within recent years and have been described by Wasmann, Donisthorpe, Emery, myself and others, can be shown to have established trophallactic relations with their host species. One of the most instructive is *Leptothorax emersoni* which lives with *Myrmica canadensis*. I have described its habits and those of one of its subspecies in three of my former papers (1901, 1903, 1907).

4. The relations of ants to plant-lice and other Homoptera and to the larvæ of Lepidoptera outside the nest are, as I have said, incompletely trophallactic, since these insects are not fed, though they may be defended by the ants. The Homoptera are not fed probably for the simple reason that their mouthparts are so peculiarly specialized for piercing plant-tissues and sucking their juices, and the Lepidopteron larvæ have, as a rule, no occasion to abandon their leaf diet. There are, however, several cases in which both caterpillars and Homoptera have entered into more intimate association with the ants. Many of the root aphids and coccids and their eggs are collected and kept by the ants in their nests, at least during certain seasons of the year. Two of the caterpillars that have acquired closer relations with the ants are so instructive, as illustrating one of the ways in which the myrmecophilous habit has been developed, that they merit more detailed description.

F. P. Dodd (1912) found that the first-stage larva of a small gray Queensland moth, *Cyclotorna monocentra*, is ectoparasitic on a Jassid Homopteron which feeds on certain trees and is attended and "milked" by an ant of the genus *Iridomyrmex*. The ant carries the parasite but not the Jassid into its nest. There the former spins a temporary cocoon and later emerges from it as a peculiar, flat, bright red (symphilic color), second stage larva, with two long tails. In this stage it subsists "solely on the ant grubs by sucking out their juices," but as in the case of *Lomechusa* in the nests of the European *Formica sanguinea*, the ant is partially recompensed for the loss of its brood. Dodd says:

Reference has been made to the caterpillars raising their terminal segments, even the small ones from the cocoons doing so. This was quite sufficient to warrant investigation. Consequently at various times I have placed them with ants and grubs under glass, in order that they could be seen to advantage and without risk of disturbance. When the anal parts are pro-

truded, an ant generally soon becomes aware of the fact and will be seen to pay these great attention. I soon noticed that a liquid, often perfectly transparent (it looks so on the blue-green ground, probably was pale bluish), is emitted, and that it is greedily drunk up by the ants. Over and over again, with and without a lens, I have seen this issue, and the ants speedily absorb it. Some ants, perhaps hungry or more enterprising than others, would take in a supply from a second caterpillar. If an ant is not satisfied with the quantity given out, she deliberately seizes the protruding parts and gives them a gentle nip, the mandibles can plainly be seen to press upon the juicy flesh; if the hint is not immediately acted upon a more vigorous squeeze is given, and the tails may be gripped and pressed. This is very comical, the ant's meaning is unmistakable and the caterpillar so thoroughly understands it, too, for a second hint never fails. This liquid, though frequently quite clear, is often mixed with yellowish matter, and at times some jelly-like substance is extruded; the latter the ants do not care about, for after the moisture is licked up this is in their way, and if they have not been imprisoned too long, will seize and tug at it until it comes off, and carry it to a spot set apart for waste matter, such as their own pellets and pupal skins, etc., are kept in.

Dodd also observed the ants licking and cleaning the caterpillar and the caterpillar cleaning the ants! When mature the caterpillar leaves the nest, travels to the nearest tree in company with the foraging ants, spins its cocoon in a crevice of the bark and pupates. In about twenty days the moth emerges.¹⁰

The second case is the caterpillar of *Lycæna orion*, which has been recently studied by Chapman (1916, 1916a) and Frohawk (1916) in England. The butterfly lays its eggs on thyme and other plants. On these the larva feeds, and is often attended by ants as it possesses a honey-gland like many other larval *Lycænids*. When it has reached the third, or last moult it crawls down to the ground and on encountering a foraging worker of *Myrmica lœvinodis* or *scabrinodis* hunches up the anterior segments of its body in a singular manner. Frohawk interprets this behavior as a "signal" which induces the ant to seize the caterpillar and carry it into the nest.

¹⁰ When I was in Queensland Dodd generously gave me a fine series of all the stages of this extraordinary insect, together with specimens of its host ant. The latter, which I had previously found regularly nesting in the superficial portions of large, flat termitaria at Koah and Townsville, is not, as Dodd states in his paper, *Iridomyrmex purpureus* Smith (= *detectus* Smith), but *I. sanguineus* Forel. It is smaller and paler than *detectus*, but every bit as fierce and aggressive.

The individual ant which first finds the larva is always the one to carry it off. Although during its attendance several other ants may find the larva and stay by it a short time, and even milk it, they soon leave it to its original attendant, who apparently informs them that their services are not needed. [!] Whether the ant signals to the larva for it to prepare itself for transit, or the larva gives the signal that it is ready to be taken, seems doubtful; but from what we have seen both Capt. Purefoy and I are inclined to think that the larva gives the signal. No. 3 larva alluded to hunched itself both the second and third time while the ant was about an inch away and facing an opposite direction, and at the fourth hunching up the ant was standing over the larva ready for the signal, and when this was given it was quickly seized and carried.

Chapman observed that after the caterpillar was taken into the nest it fed on the *Myrmica* larvæ. During this period of its life it was not seen to yield the secretion of its honey-gland but was treated by the ants as what Wasmann would call an indifferently tolerated guest, or *synœkete*.

5. The fifth expansion of trophallaxis, namely the acquisition of trophic relations with the myrmecophytes, or plants possessing extra-floral nectaries or food-bodies, is also imperfect like ordinary trophobiosis, since the ants merely obtain nutriment from the plants and possibly afford them some protection. The nectar and other plant-foods are for the purposes of the ants merely so many exudates like the excrement of the Homoptera (honey-dew) and the sweet secretions of the Lycænid caterpillars which feed on the foliage.

As the foregoing study of trophallaxis has an important bearing on Wasmann's and Holmgren's interpretation of symphily it will be advisable to consider their views in greater detail. Wasmann has elaborated his ideas in regard to the origin and meaning of symphily in several papers, but as an article published in 1910 embodies his mature and apparently final contentions, his earlier publications need not be drawn into the discussion. Having found that particular symphiles live only with particular host ants and termites, he concludes, first, that the latter have during their phylogeny acquired particular symphilic instincts as differentiations or modifications of their original nursing and adoptive instincts, and second, that the true ant and termite guests have been developed by these symphilic instincts through a process called "amical selection," which he

likens to the conscious artificial selection employed by man in perfecting the numerous, often bizarre varieties among his domesticated animals and plants. Escherich (1898, 1902, 1911), Schimmer (1909, 1910) and I (1910) have never accepted this view, and I am still unable to see that Wasmann has successfully disposed of our arguments. The whole matter comes down to the answers to two questions: Do ants and termites possess special symphilic instincts? and: Is the assumption of amical selection necessary to account for the facts? In my opinion both questions are to be answered in the negative.

It is unnecessary to consider all the various symphiles which Wasmann has so long and so carefully studied. A brief account of *Lomechusa strumosa*, his chief battle-horse and according to his own statement one of the most typical of symphiles, will suffice. This is admittedly a predatory parasite in the colonies of *Formica sanguinea*. Its larvæ devour the ant larvæ and the adult beetles are fed and licked by the ants. The fat tissue of the larva probably supplies the ants with an agreeable exudate and the adults certainly furnish an agreeable secretion from their abdominal trichome glands. When the larvæ, which are evidently treated as if they were ant larvæ, mature, they are buried in the soil, just as the ant-larvæ are buried, in order that they may pupate. The pupæ are also unearthed like the ant pupæ, after they have spun their cocoons, but this treatment is fatal to the parasites and only those that have been forgotten and left in the soil are able to develop into beetles. Often the greater part of the ant brood is destroyed by the *Lomechusa* larvæ, but in some colonies, by a process which Wasmann has never adequately explained, many of the larvæ develop into pseudogynes, or forms intermediate between workers and females. These pathological individuals are unable to perform the functions of either of the castes which they imperfectly represent. This is in its essential outlines the history of *Lomechusa*. Now Wasmann believes that *Formica sanguinea* has acquired during its phylogeny a special symphilic instinct which impels it to foster *Lomechusa* to the detriment of the colonies and therefore to the detriment of the species, and regards the case as furnishing a splendid argument against natural selection and an incontestible proof of the existence

of amical selection. The same reasoning is, of course, made to apply, *mutatis mutandis*, to *Claviger testaceus* which lives with *Lasius flavus*, the Paussids which live with different species of *Pheidole*, the physogastric Staphylinids which live with various termites, etc. The bizarre structures of these symphiles, such as the antennæ of Clavigerids and Paussids, are compared with the deformities of some breeds of domestic animals and are supposed to have arisen and to have been perfected in an analogous manner. The analogy, as conceived by Wasmann, is indeed so close that it is hard to see why the term amical selection should have been introduced for what would seem to be after all only another case of Darwin's artificial selection though performed by ants instead of men.

The argument looks plausible till we examine it more critically. When we ask how the particular symphilic instinct to foster *Lomechusa* became established *i. e.*, hereditary, in *sanguinea*, we see that Wasmann has taken a great deal for granted. Of course, we really know nothing about the phylogeny of *sanguinea* in its relation to *Lomechusa*. The *sanguinea* queen and her fertile female offspring in colonies that are old enough to be infested by the beetle, pay no particular attention to the parasite and could therefore acquire such an instinct as Wasmann postulates only by inspiration. The workers, which do look after the beetles, rarely reproduce and probably never reproduce in infested colonies and would therefore not be in a position to transmit even if they acquired such an instinct. And as the *sanguinea* brood is either largely devoured or converted into infertile pseudogynes, so that the whole colony tends to die out, we have anything but a favorable environment for engendering and transmitting an instinct so specialized as to be concerned with a particular symphile. Furthermore, *Lomechusa* is a very sporadic parasite. It may be abundant in certain regions, as in certain parts of Holland, where Wasmann has worked and at St. Moritz, in the Upper Engadin of Switzerland where I once found it and its larvæ in considerable numbers, but there are many regions in which the *sanguinea* colonies are entirely free from the pest and hence in a flourishing condition and one most favorable to the survival of the species. Wasmann has not shown that *Lomechusa* introduced into

the colonies of such regions is treated with any less consideration than in young, previously uninfested colonies in regions where the parasite is common. As *Lomechusa* is very rare in England, the experiment could be readily performed by shipping a lot of the beetles from the continent to my friend Donisthorpe, with the request that he introduce them to the British *sanguinea*. I am willing to wager that even if they came from Germany they would be hospitably licked and fed by the ants of Albion. Wasmann might, however, contend that *Lomechusa* was once a universal *sanguinea* parasite or, at any rate, much more abundant and more uniformly distributed than at present, but if this had been the case how could *sanguinea* have survived, if the ravages of the parasite are as great as he asserts, especially when we consider that *sanguinea* is itself a parasite on another ant, *Formica fusca*, and is therefore dependent on a host?

The perusal of Wasmann's papers leaves me with the impression that he is bent on showing that symphily is something biologically unique and that for every peculiarity in ant behavior we are bound to postulate a specific instinct. If three of my maiden aunts are fond of pets and prefer cats, parrots and monkeys, respectively, I am not greatly enlightened when the family physician takes me aside and informs me sententiously that my aunt Eliza undoubtedly has an ælurophilous, my aunt Mary a psittacophilous and my aunt Jane a pithecophilous instinct, and that the possession of these instincts satisfactorily explains their behavior. It is only too apparent that the physician has merely called the stimuli that severally affect my aunts by Greek names *plus* a suffix indicating "fondness," assumed their existence as entities in my aunts' minds and naïvely drawn them forth as "explanations." It is high time that such scholastic methods of conducting biological inquiries were abandoned. *Entia non sunt multiplicanda præter necessitatem* in the study of animal behavior as in other fields of research.

The observations recorded in the opening pages of this paper seem to me to constitute the most formidable argument against the existence of special symphilic instincts, for in the first place, if in the social insects the relations between parent and offspring or between the nursing workers and the offspring of the fertile females

is trophallactic, it is clearly essentially the same as the relation between host and symphile. It becomes unnecessary, therefore, to assume that in the ants and termites the primitive nursing instinct, which is a mutual feeding, has been specialized or modified during the phylogeny in adaptation to particular symphiles. Slight ontogenetic modifications, well within the limits of the plastic, or "intelligent" behavior of the ants, as responses to the specific organization of the symphiles, seem amply sufficient to account for the phenomena.

In the second place, trophallaxis is, of course, traceable to a mutualistic hunger, or "exudate hunger" as Holmgren calls it, and therefore to an appetite, in the sense in which this term is employed by English psychologists. In view of the fact that psychologists have universally regarded the appetites as very primitive and fundamental it is rather strange that they have received so little attention from the animal behaviorist. Very recently, however, Drever (1917) and Craig (1918) have emphasized their importance in connection with instinct in two valuable contributions. Drever regards the appetites as very simple or primitive instincts or "as representing an earlier stage of conscious life, which in the human being and the higher animals, is overlaid by the stage to which the development of the specific 'instinct' tendencies belong." He enumerates the hunger, thirst and sex appetites, the appetite for sleep or rest, for exercise or activity, "nausea," or "primitive disgust" and James' "instinct of personal isolation." Craig's contribution is particularly interesting because he reaches his conclusions from a study of birds (doves) and deals with the matter more thoroughly. According to him the appetites and aversions are constituents of the instincts. "Each instinct involves an element of appetite, or aversion, or both." Perhaps his view is not essentially different from Drever's, since the most typical appetites, those of hunger and sex, represent the basic reactions of organisms, and what are ordinarily called "instincts," *i. e.*, the chain-reflexes, or more elaborate mechanized behavior of animals, are evidently later and superposed activities that, so to speak, adopt the general movement or pattern of expression characteristic of the appetites. Craig, in fact, resolves the behavior of animals into cycles which run their course according to

the appetite or aversion schema. He evidently regards sexual behavior as the most typical expression of appetite. I should regard hunger as being certainly from a biological point of view the more primitive.¹¹

If we regard symphily and trophallaxis as expressions of essentially the same instinct with pronounced appetitive constituent or pattern, we can readily understand how Wasmann was led astray by the behavior of *sanguinea* towards *Lomechusa*, for the appetites are notoriously prone to perversion. In fact, Escherich's comparison of the appetite of *sanguinea* for the secretions of the beetle with alcoholism is not altogether inept. I should prefer to compare the ant's behavior with that of a cat presented with a sprig of catnip or of a leopard presented with a ball of paper sprinkled with oil of bergamot. If the secretions of the larval and adult *Lomechusa* have an analogous influence on their hosts, as is very probable, the apparently anomalous behavior of the latter would be readily understood. It would certainly be no more surprising than that my hypothetical maiden aunts prefer to have their bed-linen scented with lavender or that some of my bachelor friends prefer Havana cigars and cannot be persuaded to smoke the "domestic" variety.

If the objection be raised that I overlook the fact that the relation of *sanguinea* to *Lomechusa* is one of host to parasite, whereas that between the queen ant and her brood is one of parent to off-

¹¹ I find myself therefore in closer agreement with Jung than with Freud. The former's term "libido" seems to be practically synonymous with "appetite" in its general sense, as *e. g.*, in the following very suggestive passage (1916, p. 149): "We see the libido in the stage of childhood almost wholly occupied in the instinct of nutrition, which takes care of the upbuilding of the body." With the development of the body there are successively opened new spheres of application for the libido. The last sphere of application, and surpassing all the others in its functional significance, is sexuality, which seems at first almost bound up with the function of nutrition. (Compare with this the influence of procreation on the conditions of nutrition in lower animals and plants.) In the territory of sexuality, the libido wins that formation, the enormous importance of which has justified us in the use of the term libido in general. Here the libido appears very properly as an impulse to procreation and almost in the form of an undifferentiated sexual primal libido, as an energy of growth, which clearly forces the individual towards division, budding, etc. (The clearest distinction between the two forms of libido is to be found among those animals in whom the stage of nutrition is separated from the sexual stage by a chrysalis stage.)"

spring, I would reply that from a general biological point of view the resemblances between the two cases are still fundamental and suggestive. This has been shown by Giard in one of his interesting papers (1905, 1911). He says:

Comparative ethology permits us to go further and shows us in the clearest manner that the relations between the parent organism and its progeny are in principle absolutely the same as those which exist between a parasitized animal and its parasite and that after a period of unstable equilibrium, in which one or the other of the two organisms in contact finds itself injured to the profit of its associate, there is a tendency to establish a definitive status of mutual equilibrium in which the two partners find in their association an advantage in the struggle against the *ensemble* of common causes of destruction, both cosmic and bionomic.

A partial attainment of the equilibrium mentioned by Giard, both in the nursing relation of ants and that of *sanguinea* to *Lomechusa* is brought about by mutual feeding. In neither case is the exchange of food between the two parties quantitatively equal, but the exudates as stimuli, in all probability make up in quality or intensity for what they lack in quantity.

This brings us back to Wasmann's amical selection which still remains to be considered. It has often been remarked that the symphiles are strangely like our domestic animals in that they live in a social environment where they are protected from enemies and abundantly fed. In the case of the domestic animals Darwin long ago showed that such an environment favors the production of extraordinary variations, and Pearson (1897) and Trotter (1916) agree that when organisms unite to form larger biological units such as the Metazoan body, herds, colonies and societies, the individuals though necessarily limited in their evolution along particular lines nevertheless in other respects escape from the stabilizing influence of natural selection and exhibit unusual freedom of development and specialization. Both the domestic animals and the symphiles which really become integral members of the insect societies in which they are permitted to live, show this freedom in the development of unusual structural and color characters, as we see in albinos, peculiar breeds of fowl, pigeons and dogs, Paussids and Clavigerids with monstrous antennæ, ant-chalcids like *Kapala* and *Isomeralia*, with huge thoracic spines, etc. Similar phenomena are common in many

ecto- and entoparasites which are intimately associated with their hosts (*e. g.*, *Sacculina*, many Copepods, Isopods, tapeworms, etc.). The origin of these strange characters is evidently spontaneous, or mutational and dependent on the favorable conditions under which they arise. In the case of the domestic animals we know that the unusual characters are being continuously and rapidly perfected and established by man's selective activity. It does not follow, however, that the analogous developments of symphiles are the outcome of a similar activity on the part of the ants and termites. The resemblance of the aberrant characters of symphiles to "hypertelic" structures in many other insects has been noticed by Dahl. That the phenomena in both cases are due to the same cause, *i. e.*, the relaxation or suppression of natural selection, is much more probable than Wasmann's contention that the ants take the same interest in breeding Paussids and Clavigerids with extraordinary antennæ that we do in breeding lop-eared rabbits and fan-tail pigeons. Nor is there any evidence that even the biologically useful characters of the symphiles, namely their trichome glands and exudate tissues, are engendered or perfected by amical selection. The truly amazing cases of convergent or parallel development of these structures in symphiles belonging to the most diverse genera is, in all probability, attributable to the adaptive activities of the symphiles themselves, just as we attribute the convergent development of hooks, suckers, hermaphroditism, blindness, etc., in entoparasitic worms or aptery in ectoparasitic insects, such as lice, fleas, Polycetenids, Nycteribids, etc., to the parasites themselves and not to specifically selective efforts on the part of the host organisms.

Holmgren accepts Wasmann's amical selection and carries it a step further in his contention that it accounts for the development of the various castes in the termite colony. He says (1909, p. 200):

If now the above described connection between feeding and exudate secretion holds good, so that the quantity of exudate secretion determines the kind of feeding, it would seem to be self-evident that the exudate secretion is intimately connected with the development of castes, for Grassi and Sandias have shown that feeding is probably to be regarded as a factor in caste development. And if, therefore, the exudate secretion is the cause of feeding we must regard it as the cause of the differentiation of the various castes.

That this opinion is no longer tenable, at least in the form in which it is stated, is shown by the observations of Bugnion (1912), who has proved that the soldier and worker castes of *Eutermes* are determined in the egg, and the observations of Miss Thompson (1917), who has been able to distinguish the sexual from the sterile castes of *Leucotermes flavipes* at the time of hatching. Holmgren's thesis could be accepted only on the assumption that the effects of feeding had been carried back during the long phylogeny of the termites into the embryonic stages. Incidentally it may be said that his other statement in regard to the development of the complemental or neotenic males and females in the termite colony refer, not to the development of castes, but to the ontogenetic growth of the exudate tissues, a process which is exhibited in the most extraordinary manner during the imaginal life of the true queens of many species.

In conclusion it may be interesting to note in connection with the development of the social habit of insects from a trophallactic relation between parent and progeny, that the social or gregarious instinct in man has also been regarded by some authors as an appetite. Drever (1917) cites the early British philosopher Hutcheson ("Nature and Conduct of the Passions," Sect. 4, 1728) as classifying the gregarious instinct among the appetites, and referring to McDougal's interesting comments on gregariousness (1910), he says (p. 184):

There is in the instinct itself something which suggests such a view [as McDougal's], something which might even lead the psychologist to maintain that it belongs to the "Appetite" group in our system of classification, an opinion to which Galton's description [of the wild ox of Damaraland which cannot endure even a momentary severance from the herd] would lend some support. There is indeed something primordial about the whole experience involved in the operation of the gregarious instinct.

The fact that higher gregarious and social animals are satisfied as long as they are with their fellows but become uneasy when isolated is certainly very suggestive of the appetitive type of behavior.¹² In

¹² As Trotter says (1916). "In interpreting into mental terms the consequences of gregariousness, we may conveniently begin with the simplest. The conscious individual will feel an unanalyzable primary sense of comfort in the actual presence of his fellows, and a similar sense of discomfort in their absence. It will be obvious truth to him that it is not good for the man to be alone. Loneliness will be a real terror, insurmountable by reason."

this connection some of Le Dantec's recent writings are of considerable interest. In a footnote (p. 288) at the end of "Les Influences Ancestrales" (1917) he asks:

Does maternal love, which has assumed such great moral significance in the human species, originate among the females of the Mammalia as the desire (*souci*) to rid themselves of their milk?

A similar tendency to show that the social relation in man has an egoistic instead of an altruistic foundation is even more forcibly displayed in his startling not to say shocking, volume entitled "L'Égoïsme Seule Base de Toute Société" (1916).¹³

BIBLIOGRAPHY.

1914. Arnold, G. Nest-Changing Migrations in Two Species of Ants. *Proc. Rhodes. Sc. Assoc.*, 13, 1914, pp. 25-32, 1 pl.
 1901. Berlese, A. Osservazioni su Fenomeni che avvengono durante la Ninfosi degli Insetti Metabolici. *Rivist. de Patol. Veget.*, 8, 1901, pp. 1-155, 6 pls., 42 text-figs.; 10, 1901, pp. 1-120, 8 pls., 5 text-figs.

¹³ Since the foregoing paragraphs were written I have found two quotations from Charles Bonnet's "Contemplation de la Nature," which are the more remarkable because they were published in 1764. On p. 213 he says: "In order the better to insure the well-being of their progeny, would not Nature have engaged the affection of the mothers in such a manner that the young would become for them a source of agreeable sensations and material usefulness? Certain facts seem to confirm this conjecture. . . . The mammæ have been constructed with such art that the sucking and pressure exerted by the young excite the nerves which impart to these organs a delicate disturbance or soft commotion accompanied by a feeling of pleasure. This pleasure sustains the natural affection of the mother, if indeed it be not one of its principal causes. The same may be said of the action of licking, which is reciprocal. Finally, mothers are sometimes incommoded by the abundance of their milk; the young relieve them by sucking." The second quotation (p. 272) is even more astonishing in its bearing on the conditions in the social insects: "The neuters [of bees] have no sex and do not reproduce. How can we suppose that they have the same affection for the offspring of their queen as the mothers of other animals? They behave nevertheless in the same manner under the same circumstances. If, therefore, Nature has known how to insure the attachment of mothers by the agreeable sensations derived from their offspring or by the services they render, it would certainly seem that she must employ much the same means in the case of the worker bees and that she has placed in the young a secret source of delectable sensations which attaches them to the workers and induces them to disgorge into the cells the kind of porridge with which the young are nourished." These quotations are from a work entitled "La Psychologie Animale de Charles Bonnet" published in 1909 in Geneva by Ed. Claparède who cites them and the work of Giard in support of his views on the reciprocal relations of the mother to her offspring.

1909. Berlese, A. Gli Insetti, 1, 1909, p. 535, figs. 618, 619.
1902. Biedermann, W. Ueber die Struktur des Chitins bei Insekten und Crustaceen. *Anat. Anzeig.*, 21, 1902, pp. 485-490.
1903. Biedermann, W. Geformte Secrete. *Zeitschr. f. allgem. Physiol.*, 2, 1903, pp. 395-481, 4 pls.
1894. Bordas, L. Appareil Glandulaire des Hyménoptères. *Ann. Sc. Nat. Zool.* (7), 19, 1894, pp. 1-362, 11 pls.
1902. Brauns, H. Eucondylops n. g. Apidarum. *Zeitschr. Syst. Hym. Dipt.*, 2, 1902, pp. 379-380.
1912. Bugnion, E. Observation sur les Termites. Différentiation des Castes. *Compt. Rend. Soc. Biol.*, Paris 1, 1912, pp.
- 1903, 1905. du Buysson, R. Monographie des Guêpes ou Vespa. *Ann. Soc. Ent. France*, 72, 1903, p. 260; *ibid.*, 74, 1905, p. 485.
1913. Casper, A. Die Körperdecke und die Drüsen von *Dytiscus marginalis* L., ein Beitrag zum feineren Bau des Insektenkörpers. *Zeitschr. f. wiss. Zool.*, 107, 1913, pp. 387-508, 44 text-figs.
1916. Chapman, T. A. What the Larva of *Lycæna orion* does during its Last Instar. *Trans. Ent. Soc. Lond.*, 1916, pp. 291-297, 9 pls.
- 1916a. Chapman, T. A. Observations Completing an Outline of the Life History of *Lycæna orion* L. *Trans. Ent. Soc. Lond.*, 1916, pp. 298-312, 3 pls.
1918. Craig, W. Appetites and Aversions as Constituents of Instincts. *Biol. Bull.*, 34, 1918, pp. 91-107.
1889. De Bono, F. P. Sull' umore segregato della *Timarcha pimelioides* Schæffer. *Natural. Sicil.*, 8, 1889.
1912. Dodd, F. P. Some Remarkable Ant-friend Lepidoptera of Queensland. *Trans. Ent. Soc. Lond.*, 10, 1912, pp. 577-590, 1 pl.
1917. Drever, J. Instinct in Man, a Contribution to the Psychology of Education. Cambridge University Press, 1917.
1898. Escherich, K. Zur Anatomie und Biologie von *Pausus turcicus* Friv. *Zool. Jahrb. Abt. Syst.*, 12, 1898, pp. 27-70, 1 pl., 11 text-figs.
1902. Escherich, K. Biologische Studien über algerische Myrmekophilen zugleich mit allgemeinen Bemerkungen über die Entwicklung und Bedeutung der Symphylie. *Biol. Centralbl.*, 22, 1902, pp. 638-663, 4 figs.
1911. Escherich, K. Termitenleben auf Ceylon. Jena, Gustav Fischer, 1911.
1899. Emery, C. Intorno alle Larve di Alcune Formiche. *Mem. R. Accad. Sc. Ist. Bologna* (5), 8, 1899, pp. 3-10, 2 pls.
- V 1912. Emery, C. Études sur les Myrmicinae. *Ann. Soc. Ent. Belg.*, 56, 1912, pp. 94-105, 5 figs.
1901. Fielde, A. M. A Study of an Ant. *Proc. Acad. Nat. Sc. Phila.*, 53, 1901, pp. 425-449.
1890. Forel, A. Un Parasite de la *Myrmecia forficata* Fabr. *Compt. Rend. Soc. Ent. Belg.*, 1890, p.

1914. Friese, H. Bienenlarven mit Pseudopodien und neue Arten der Gattung Allodape. *Deutsch. Ent. Zeitschr.*, 1914, pp. 144-146, 1 fig.
1916. Frohawk, F. W. Further Observations on the Last Stage of the Larva of *Lycæna orion*. *Trans. Ent. Soc. Lond.*, 1916, pp. 313-316, 2 pls.
- 1905, 1911. Giard, A. Les Origines de l'Amour Material. *Bull. Inst. Psych. Internat.*, 5, 1905, p. 1; *Revue des Idées*, 1905, p. 249; Republished in Giard's "Œuvres Diverses," 1, 1911, pp. 207-235.
1901. Holmgren, N. Ueber das Verhalten des Chitins und Epithels zu den unterliegenden Gewebearten bei Insekten. *Anat. Anzeig.*, 20, 1901, pp. 480-488.
1902. Holmgren, N. Ueber die morphologische Bedeutung des Chitins bei den Insekten. *Anat. Anzeig.*, 21, 1902, pp. 373-378, 5 figs.
1909. Holmgren, N. Termitenstudien I. Anatomische Untersuchungen. *K. Svensk. Vetensk. Handl.*, 44, 1909, pp. 1-215, 3 pls., 75 text-figs.
1903. Janet, C. Observations sur les Guêpes. Paris, Carré et Naud, 1903.
1913. Jordan, H. C. Zur Morphologie und Biologie der myrmecophilen Gattungen *Lomechusa* und *Atemeles* und einiger verwandter Formen. *Zeitschr. f. wiss. Zööl.*, 107, 1913, pp. 346-386, 20 text-figs.
1916. Jung, C. G. Psychology of the Unconscious. Transl. by Beatrice M. Hinkle. New York, Moffat, Yard & Co., 1916.
1911. Kapzov, S. Untersuchungen über den feineren Bau der Cuticula bei Insecten. *Zeitschr. f. wiss. Zööl.*, 98, 1911, pp. 297-337, 3 pls., 3 text-figs.
1898. Karawaiew, W. Die Nachembryonale Entwicklung von *Lasius flavus*. *Zeitschr. f. wiss. Zööl.*, 64, 1898, pp. 385-478, 4 pls., 15 text-figs.
1910. Krüger, E. Beiträge zur Anatomie und Biologie des Claviger testaceus Preysl. *Zeitschr. f. wiss. Zööl.*, 95, 1910, pp. 327-381, 2 pls., 33 text-figs.
1916. Le Dantec, F. L'Égoïsme Seule Base de Toute Société. Paris, Ern. Flammarion, 1916.
1917. Le Dantec, F. Les Influences Ancestrales. Paris, Ern. Flammarion, 1917.
1895. Lutz, K. G. Das Blut der Coccinelliden. *Zööl. Anzeig.*, 18, 1895, pp. 244-255.
1910. McDougall, W. An Introduction to Social Psychology. 2d Ed., Boston, J. W. Luce & Co., 1910.
1881. Magretti, P. Del Prodotto di Secrezione Particolare di Alcuni Meloidi; Esame Microscopico. *Bull. Scient. Pavia*, 3, 1881, p. 58.
1882. Magretti, P. Ricerche Microscopiche sopra i Liquidi di Secrezione e di Circolazione nelle Larve di Alcuni Imenotteri Tentredinei. *Boll. Scient. Pavia*, 4, 1882, p. 58.
1897. Pearson, K. The Chances of Death and Other Studies in Evolution. 2 vols. London, New York, E. Arnold, 1897.

1902. Pérez, C. Contribution a l'Étude des Métamorphoses. *Bull. Scient.*, 37, 1902, pp. 195-427, 3 pls.
1913. Reichensperger, A. Zur Kenntnis von Myrmecophilen aus Abessinien. *Zoöl. Jahrb. Abt. f. Syst.*, 35, 1913, pp. 185-218, 2 pls., 15 text-figs.
1908. Roubaud, E. Gradation et perfectionnement de l'instinct chez les Guêpes Solitaires d'Afrique, du genre *Synagris*. *Compt. Rend. Acad. Sc.*, 147, 1908, pp. 659-697.
1910. Roubaud, E. Recherches sur la Biologie des *Synagris*. Evolution de l'Instinct chez les Guêpes Solitaires. *Ann. Soc. Ent. France*, 79, 1910, pp. 1-21, 4 pls.
- 1910a. Roubaud, E. Aperçus biologiques sur les Guêpes Sociales d'Afrique des Genres *Icaria* et *Belonogaster*. *Compt. Rend. Acad. Sc.*, 1910, pp.
1916. Roubaud, E. Recherches Biologiques sur les Guêpes Solitaires et Sociales d'Afrique. *Ann. Sc. Nat. Zoöl.* (10), 1, 1916, pp. 1-160, 34 figs.
1914. Santschi, F. Formicidæ in "Voyage de Ch. Alluaud and R. Jeannel en Afrique Orientale (1911-1912)," *Ins. Hymen.*, 2, 1914, pp. 43-148, 2 pls., 30 text-figs.
1909. Schimmer, F. Beitrag zu einer Monographie der Gryllodeengattung *Myrmecophila* Latr. *Zeitschr. f. wiss. Zoöl.*, 93, 1909, pp. 409-534, 3 pls., 29 text-figs.
1910. Schimmer, F. Ueber die Wasmannische Hypothese des "Duldungsinstinktes" der Ameisen gegenüber synöker Myrmecophilen. *Zoöl. Anzeig.*, 36, 1910, pp. 81-95.
1912. Sladen, F. W. L. The Humble-Bee, its Life-History and how to Domesticate it. London, Macmillan & Co., 1912.
- 1737, 1738. Swammerdam, J. *Biblia Naturæ, sive Historia Insectorum*, etc 2 vols. Leydæ, Severin, etc. 1737, 1738.
1917. Thompson, Caroline B. Origin of the Castes of the Common Termite, *Leucotermes flavipes* Kol. *Journ. Morph.*, 30, 1917, pp. 83-136, 8 pls., 5 text-figs.
1907. Trägårdh, I. Description of *Termitomimus*, a New Genus of Termitophilous Physogastric Aleocharini, with Notes on its Anatomy. *Zoöl. Studier.*, Upsala, 1907, pp. 172-190, 1 pl., 10 text-figs.
- 1907a. Trägårdh, I. Notes on a Termitophilous Tineid Larva. *Ark. f. Zoöl.*, 3, 1907, pp. 1-7, 1 pl.
1916. Trotter, W. *Instincts of the Herd in Peace and War*. New York, Macmillan Company, 1916.
1903. Wasmann, E. Zur näheren Kenntnis des echten Gastverhältnisses (Symphilie) bei den Ameisen- und Termitengästen. *Biol. Centralbl.*, 23, 1903, pp. 63-72, 195-207, 232-248, 261-276, 298-310, 25 text-figs.
1910. Wasmann, E. Ueber das Wesen und den Ursprung der Symphilie. *Biol. Centralbl.*, 30, 1910, pp. 97-102, 129-138, 161-181.

1915. Wasmann, E. Neue Beiträge zur Biologie von *Lomechusa* und *Atemeles* mit kritischen Bemerkungen über das echte Gastverhältnis. *Zeitschr. f. wiss. Zool.*, 114, 1915, pp. 233-402, 2 pls., 1 chart and 2 text-figs.
1890. Wheeler, W. M. On the Appendages of the First Abdominal Segment of Embryo Insects. *Trans. Wis. Acad. Sc. Arts. Lett.*, 8, 1890, pp. 87-140, 3 pls.
1900. Wheeler, W. M. A Study of Some Texan Ponerinæ. *Biol. Bull.*, 2, 1900, pp. 1-31, 10 figs.
- 1900a. Wheeler, W. M. The Habits of *Ponera* and *Stigmatomma*. *Biol. Bull.*, 2, 1900, pp. 43-69, 8 figs.
1901. Wheeler, W. M. An Extraordinary Ant-Guest. *Amer. Natural.*, 35, 1901, pp. 1007-1016, 2 figs.
- 1901a. Wheeler, W. M. Compound and Mixed Nests of Ants. *Amer. Natural.*, 35, 1901, pp. 431-448, 513-539, 701-724, 791-818, 20 figs.
1903. Wheeler, W. M. Ethological Observations on an American Ant (*Leptothorax emersoni* Wheeler). *Arch. Psych. Neurol.*, 2, 1903, pp. 1-31, 1 fig.
1907. Wheeler, W. M. Notes on a New Guest Ant, *Leptothorax glacialis*, and the Varieties of *Myrmica brevinodis*. *Bull. Wis. Nat. Hist. Soc.*, 5, 1907, pp. 70-83.
1907. Wheeler, W. M. The Polymorphism of Ants, with an Account of Some Singular Abnormalities Due to Parasitism. *Bull. Amer. Mus. Nat. Hist.*, 23, 1907, pp. 1-92, 6 pls.
1910. Wheeler, W. M. Ants, Their Structure, Development and Behavior. New York, Columbia University Press, 1910.
1915. Wheeler, W. M. On the Presence and Absence of Cocoons Among Ants, the Nest-Spinning Habits of the Larvæ and the Significance of the Black Cocoons Among Certain Australian Species. *Ann. Ent. Soc. Amer.*, 8, 1915, pp. 323-342, 5 figs.